

If they like, the authors of "Standardized Plant Names" may reply to the comments on "that presumptuous model." Its saving grace is that when a student sees the names osageorange, tanoak, and pineapple, he knows that the first is not an orange, the second is not an oak, and the third is not an apple. By the way, does the reviewer spell pineapple "pine" "apple" and if not, why not?

Evidently the author's primary error was in sending a copy of the key to "Rhodora" for review. It was his misconception that the magazine was actually "devoted primarily to the flora of the Gray's Manual Range and regions floristically related." In his opinion, a key based upon fruit characters fell within these limits.

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## GENERIC STATUS OF TRIODANIS AND SPECULARIA

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IN RHODORA for September, 1946, Professor M. L. Fernald discussed in detail the case of "*Triodanis* versus *Specularia*"<sup>1</sup>, concluding that as a genus *Triodanis* "seems . . . very weak." He advocated the reunion of *Triodanis* with the European genus *Specularia*, in accordance with the policy established by Alphonse DeCandolle in 1830 and subsequently followed by practically all European workers and most Americans. Professor Fernald's conclusions were reached after examination of my earlier paper on *Triodanis*<sup>2</sup>, and his objections to the maintenance of the group as an independent genus were based chiefly upon what he called the "reputed generic differences" which he understood to be summarized in two paragraphs of this earlier paper. He felt that these "differences" did not include constant strong morphological characters, and he considered that some of them had been over-stressed or were, indeed, meaningless as set forth. He showed to his own satisfaction that *Triodanis* was not to be considered "a clearly distinct genus" (that is, distinct from *Specu-*

<sup>1</sup> RHODORA 48: 209-214, 215, 216. pl. 1049, 1050.

<sup>2</sup> Wrightia 1: 13-52. 1945.

*laria*), but apparently he did not consider what I believe to be the main issue, the existence of either *Specularia* or *Triodanis* as a real entity apart from *Campanula*.

The case for *Triodanis* has already been set forth at length, in the paper referred to above, but I think it worthwhile to reopen the discussion here in the pages of RHODORA, because of my own conviction that *Triodanis* constitutes a biologically coherent group of species which is as well founded as most genera of the *Campanulaceae* and which should be recognized as an independent genus. One infers from Professor Fernald's article that *Specularia* will be used in the traditional, inclusive sense, in the forthcoming 8th edition of "Gray's Manual," and it would seem unfortunate to have this generic name perpetuated indefinitely, through the undoubtedly enormous influence of the "Manual," without some further examination of the qualifications of the genus.

In the first place it may be reiterated that there is no justification whatever for maintaining *Specularia*, in its traditional circumscription, as a genus apart from *Campanula*. It is neither sharply delimited nor homogeneous, and its components are evidently less closely akin to one another than to *Campanula* itself. If the inclusive *Specularia* be dismembered, however, as suggested previously<sup>1</sup>, and restricted to the type-species and one other, it may be maintained as a weak segregate from *Campanula*. To quote my own words (*Wrightia*, l. c.): "The desirability of recognizing *Specularia* as a genus is still [after dismemberment] open to question, but the combination of divided corolla, elongated capsule and glabrous filaments is unique among the annual species of the *Campanula* complex, and these similarities may indicate some generic affinity between the two entities involved [i. e. the two original species of *Specularia*, *S. Speculum-Veneris* and *S. hybrida*], although these [species] are superficially dissimilar in aspect, degree of branching, and size and shape of flowers".

The weakness of *Specularia* as a genus was recognized by Alphonse DeCandolle, whose *Monographie des Campanulées* (1830) has been the foundation for all subsequent work on the *Campanulaceae*. Of the species of *Specularia* DeCandolle wrote (*Monographie*, p. 46, here translated from the original French):

<sup>1</sup> *Wrightia* 1: 17. 1945.

“They form a group very near the Campanulas, and distinct more by the habit than by any positive characters”. He went on to explain that in spite of analogies between species of *Specularia* and similar species in *Campanula*, he had experienced no difficulty in distinguishing the two genera “except for the one species *C. fastigiata* Duf., which is so intermediate, in habit and other characters, that one can at will place it in the one genus or the other”. One certainly cannot quote DeCandolle in support of insistence upon strong morphological characters as generic criteria in the *Campanulaceae*!

It is worthwhile here to examine in some detail the philosophical concepts employed by DeCandolle in delimiting the genera of *Campanulaceae*, since his *Monographie* remains the latest significant or original work on the family as a whole. The compilations of Endlicher, Bentham & Hooker, and Schönland, as far as these relate to the *Campanulaceae*, are taken over from DeCandolle’s work without any important changes. Endlicher’s *Genera* (1838) followed the *Monographie* even as to the sequence of genera, and without any change in generic concept. Bentham & Hooker (*Genera*, vol. 2, part 2, 1876) accepted DeCandolle’s genera as delimited by him, except that they submerged the monotypic *Petromarula* in *Phyteuma*, explaining its earlier separation on the basis of mistaken observation on the part of DeCandolle. Schönland likewise (in Engler & Prantl, *Natürl. Pflanzenf.* 4: part 5, 1894), used DeCandolle’s genera essentially unchanged; like Bentham & Hooker he added certain genera discovered since 1830, and like them he submerged *Petromarula*.

In writing on the delimitation of genera DeCandolle was emphatic that he did not set up these groups merely because they could be separated from related groups by arbitrary characters; to him a genus was a natural unit, recognizable by its own combination [“*ensemble*”] of features. The coherent anthers of *Symphyandra* were not enough in themselves to establish the group as a genus; he pointed out (*Monographie*, p. 47) that it was “besides natural enough as to habit and other characters”. He summed up his practice in the following words (p. 64): “I have not kept or established any genus which was not founded at the same time on positive characters and on the habit [*le port*], or, in other words, on the reproductive organs and those of vegetation”.

In the case of *Specularia*, as he said himself, the genus depended more upon the habit than upon the positive characters! Nor is this the only case in point: of *Platycodon* and *Microcodon* he wrote that these were not separated by any strong characters (p. 63), but “unhappily, their habit is so different that one is forced thereby to make two distinct genera”. Yet *Specularia*, *Platycodon* and *Microcodon*, founded as they were without any strong morphological basis, but recognizable chiefly by their *ensembles* of characters, were accepted without question by Endlicher, Bentham & Hooker, and Schönland.

DeCandolle was fully aware that the genera of *Campanulaceae* are interrelated in a reticulate pattern (*Monographie*, p. 64). He pointed out that the ill-defined genus *Campanula* constitutes a sort of center in the group to which it belongs: “[It] has around it the genera *Specularia*, *Adenophora*, *Symphyandra* and *Michauxia*, which are very close to it [*qui en sont très rapprochés*], and which touch at each of its subdivisions . . . All are closer [*plus voisins*] to the genus *Campanula* than to one another. Thus whatever linear series be adopted, it will necessarily be imperfect on this point.” I am in full agreement with the thought expressed in this quotation, and to the genera enumerated by DeCandolle I should add *Triodanis*; whether it be considered an independent genus or not, it seems no more closely related to *Specularia* (in the restricted sense) than to other annual species of *Campanula*. This was discussed in *Wrightia* (l. c.), and some of the following discussion bears on the same question.

The above remarks should be enough to make clear my first point, which has to do with the manner of delimitation of genera in the *Campanulaceae*. The genera in this family stand independently only when their coherence makes them biological units, recognizable to us by some combinations of characters which do not appear elsewhere in the family. There are a few genera like *Adenophora* and *Downingia* which are possessed, in addition, of distinctive morphological characters, sufficient without any additional evidence to set these genera apart. There are also some 30 monotypic genera which are unique or not according to the opinions of individual systematists, and which are founded for the most part upon single characters of doubtful or minor import. In the great majority of cases, however, the most important thing

about each genus, from the standpoint of classification, is its own existence as an entity, not some arbitrary and possibly quite meaningless difference between it and some other group. The genera of *Campanulaceae*, much as we should like them to constitute natural biological groups, are still more or less artificial, delimited partly for the sake of convenience (we do not know, for example, that the coherent anthers of *Symphyandra* have any particular phylogenetic significance, but it is convenient and apparently natural to assemble under this name all the species having this character), and nothing can improve our system of classification more than full realization of this. If we are to depend upon what may be called the method of delimitation of genera by separation, by splitting blocks off the corners of some larger mass, by arbitrary quantitative differences which are easily measured and applied to limited numbers of specimens, then we shall lose sight of the biological implications of classification. In contrast it is possible usually to delimit genera most satisfactorily as it were by accretion, by building around natural centers of population as determined by studies of morphology or by the use of whatever techniques may be available. With emphasis placed upon similarities and affinities, rather than upon differences, it should be possible for systematists to arrive at schemes of classification more generally acceptable to their colleagues and to the general public.

The above applies specifically to the *Campanulaceae* (including the *Lobelioideae*), but I judge that it is equally applicable to most other plant-families, or perhaps to all of them. *Fragaria*, for example, is none too solidly founded on morphological grounds; it is, in fact, about as distinct from *Potentilla* as *Triodanis* from *Campanula*. But what could constitute a better genus than *Fragaria*, homogeneous as it is, and comprising several species all exhibiting the same combinations of traits? Examples of similar cases in other plant-families could be multiplied, but note merely how it applies to *Triodanis*; again the following quotation is from *Wrightia*: "The combination of annual habit, deeply divided corolla, capsule longer than wide and opening near the apex, spicate inflorescence, and regular production of cleistogamous flowers at the lower nodes is a unique one, and when found in a relatively large number of species surely points to a genetic dis-

continuity that may be called a generic distinction". The characters of *Triodanis* individually are not particularly strong; each of them (with the possible exception of the pattern and rhythm of the cleistogamy) has its counterpart or near-counterpart in *Campanula*. There is thus no sharp break between *Triodanis* and *Campanula*, but neither is there a sharp break between *Aster* and *Erigeron*<sup>1</sup>; there IS such a hiatus between *Triodanis* and *Specularia*, but none between the latter and *Campanula*. Neither *Specularia* nor *Triodanis* can be maintained as genera distinct from *Campanula* except through primary emphasis on the stature given them by their collective features, but if one wishes he can distinguish technically between the two as follows, understanding that the differentiating characters are quite possibly minor ones which CONFIRM rather than AFFIRM the generic distinction emphasized by the *ensemble*:

TRIODANIS: Filaments ciliate at base; central flowering axis and those of the main branches spicate; flowers at the lower fertile nodes prevalingly cleistogamous.

SPECULARIA: Filaments glabrous; plants normally diffusely branched, the flowers clustered near the tips of the branches or corymbosely aggregated at the summit of the plant; flowers all corolliferous.

With the above in mind, we may consider some of the morphological characters which together define *Triodanis* and *Specularia*, in the light of Professor Fernald's remarks. Before any detailed consideration I must make public apology for careless presentation in my earlier paper. On pages 13 to 20 of the first volume of *Wrightia* were set forth what I took to be sufficient technical data and philosophical considerations to justify the acceptance of *Triodanis* as a genus. To these were added, on pages 20 and 21, synopses to facilitate comparison of the features of *Campanula*, *Heterocodon*, *Specularia*, and *Triodanis*. These synopses emphasized not only differences between the genera but also qualifying and parallel conditions. They were not intended, as Professor Fernald seems to have assumed, to stress individual diagnostic characters; nor were they for use as a key to genera, as their perhaps unfortunate position at the beginning of the section entitled "Systematic Treatment" may have indicated. My own position in the matter was clearly stated, although evi-

<sup>1</sup> See Cronquist's remarks on this, in *Brittonia* 6: 122-123. 1947.

dently not sufficiently emphasized, on page 20: "It will be noted [i. e. in the following synopses] that the generic characters of the groups segregated from *Campanula* are all weak ones, in no case involving strong morphological features which absolutely separate them from the more inclusive genus, but always depending upon combinations of weaker characters which reappear individually in unrelated species of *Campanula*".

I must make further apology for not describing more precisely what Professor Fernald implies is a sort of neo-Rafinesquian distinction. This is the matter of the quite different types of branching exhibited by species of *Triodanis* and *Specularia*, respectively. In contrasting these two groups, I carelessly omitted mention of the rather obvious fact that both branch freely from the very base or near it, when the plants are growing under favorable conditions. As Professor Fernald infers, this type of branching is to be expected in annual weedy plants, and is of no importance as a taxonomic character in this case. Quite different, however, is the branching of the central flowering axis, which is spicate in *Triodanis* and corymbosely branched in *Specularia*. It is true that the growth of lateral branches in *Triodanis coloradoensis* may obscure the "racemose" condition of the axis, but this last may still be discerned on most of the branches in specimens except vigorous old fruiting plants; even in these, as in Professor Fernald's plate designed to show the opposite condition (plate 1050), the "racemose" tendency is evident on the lower branches. It is of course to be remembered that truly racemose branching does not occur in the *Campanulaceae* proper, the spike of *Triodanis* being apparently a derived inflorescence-type which is fundamentally determinate, and in which the single-flowered nodes are so because of abortion of potentially active branch-buds below the terminal ones, each solitary axillary flower representing an axillary branch reduced to this extent. Under conditions favorable for growth these branches may elongate and produce several flowers, or branch again, excessive stimulation occasionally causing the development of plants suggesting some really different species<sup>1</sup>. The branching of *Triodanis*, as discussed in *Wrightia* (l. c. 23-24), follows a definite pattern but evidently

<sup>1</sup> As in *Campanula americana*, a species with a spicate inflorescence very similar to that of *Triodanis*; see *Bartonia* 23; 37-39. 1945.

is not fundamentally different from that of other campanulaceous genera. It serves none the less as an important diagnostic character if it be remembered that it may be influenced by environment, although primarily under genetic control.

The branching in *Specularia* (as the genus was restricted in *Wrightia*, is essentially like that in many other annual campanulaceous plants. Branches from the upper axils are the rule rather than the exception, so that the flowers are usually in small groups or solitary at the tips of slender branches, the whole forming a diffuse or clustered but definitely branched inflorescence, and the terminal flower often being exceeded by the growth of the lateral branches and more or less immersed in the inflorescence. The "racemose" condition is approached, as it may be in most annual and many perennial species of *Campanula*, in imperfectly developed plants. Through the kindness of Dr. Charles Baehni, I have seen the Gittard specimen cited by Boissier (*Fl. Orient.* 3: 959. 1875) as the type of *Specularia Speculum*, var. *racemosa*, to which Professor Fernald refers. The plant is not a stunted or starved specimen, as I had speculated, but one in which the usual lateral branches from the upper part of the main axis are all equally very short (3–5 mm. long) and tipped each with a cluster of 3 or 4 flowers. The resulting inflorescence is "racemose" about to the same extent as that of *Solidago Virga-aurea*; it is long and slender, with numerous short flowering branches. It is by no means "ut in *Sp. falcata* racemosa" as Boissier said, unless one wishes to stress (it seems to me unduly) the homology between the normally reduced, one-flowered branches of the "raceme" of *Sp. falcata*, and the abnormally reduced, several-flowered branches of this one specimen of *Sp. Speculum-Veneris*. I take it that the strength or weakness of any genus lies in what its species usually or regularly have in common, not in abnormal plants which may vary markedly in one character or another from their closest relatives. Such aberrant individuals may offer valuable clues in regard to past evolutionary connections between species or genera, or in regard to evolutionary tendencies, but hardly suffice in themselves to determine generic limits in present-day populations.

Professor Fernald argues that the mere existence of cleistogamy



in *Triodanis* is not enough in itself to justify the separation of *Triodanis* and *Specularia*. He cites several genera in different plant-families, suggesting that in *Utricularia*, *Panicum*, *Viola*, and *Danthonia* the mere occurrence of this trait in certain species does not justify the generic segregation of these species from the more inclusive groups. He is of course amply justified in this view, but strict analogy and adherence to his expressed views would then suggest the union of *Triodanis* not with *Specularia* but with *Campanula*, where cleistogamy does occur in some species (as far as I am aware, no one has suggested that these should be separated off as a distinct genus because of this one trait!). It is of course not the mere occurrence of cleistogamy but the unique pattern of its development in *Triodanis*, when correlated with other characters, that is noteworthy. Many individual plants of *Triodanis coloradoensis*, for example, produce all corolliferous flowers, but the many others that show cleistogamy follow the development-pattern of the other species of the genus, indicating their biological affinity to these rather than to *Specularia*, in which the approach to the cleistogamous condition appears to be analogous, rather than homologous, to that in *Triodanis*.

In the past the principal supposed distinction between *Specularia* and *Campanula* has been in the capsule, that of the former genus often having been referred to as cylindrical, or oblong, or perhaps most often as linear (the latter by Boissier, l. c. 958, by Bentham & Hooker, l. c. 562, and by McVaugh, l. c. 21). Professor Fernald truly points out that there is great variation in the capsules of these species; actually one can find in almost any species of *Specularia* or *Triodanis* individual plants which have the supposed (relatively) broader capsules of *Campanula*, or the narrower ones of the segregate genera. One can not with reason remove either genus from *Campanula* (or separate them from each other) on the basis of capsule-shape. The character is of little use except in descriptive matter, and I regret that my earlier paper did not make this clear even to the superficial reader.

It is worth noting, since the recognition or non-recognition of a given genus depends so largely upon tradition and the weight of authority, that in maintaining *Triodanis* one does not necessarily label himself a disciple of the eccentric Rafinesque. The recog-

dition of the American "Specularias," as a group distinct from the European ones, seems to have begun with DeCandolle (*Monographie*, p. 47, 351), who felt that the one American species recognized by him constituted a "distinct section" (to which he gave no name). It may be argued, if one cares to resort to a syllogism, that this section occupied a place in DeCandolle's scheme of classification approximately equivalent to those occupied by sections in other genera (e. g. Sect. *Edraiantha* of *Wahlenbergia*, and Sect. III of *Phyteuma*)—sections that were soon recognized as independent genera. The astute Boissier, for example, maintained *Edraianthus* as a genus in the *Flora Orientalis*, and took up George Don's name *Podanthum* for what DeCandolle had regarded as a section of *Phyteuma*. Both *Edraianthus* and *Podanthum* (i. e. *Asyneuma* according to current rules of nomenclature) are now widely accepted as good genera. Whether or not this strengthens the case for the recognition of *Triodanis*, the fact remains that the group received a formal designation in Endlicher's *Genera* in 1838 (*Specularia*, sect. *Dysmicodon*). Thomas Nuttall, who knew the American flora well and was by no means without judgment, soon elevated this section to generic rank as his genus *Dysmicodon*<sup>1</sup>. In support of this view he said: "Nearly allied to *Specularia*, but with a different habit, calyx and seed; and with the lower flowers apetalous and reduced in the number of their parts". In the same paper Nuttall went so far as to propose a second segregate (as he thought from *Specularia*), comprising one species, *Campylocera leptocarpa*. This genus he supposed to be founded chiefly upon the unilocular, laterally dehiscent capsules of most of the imperfect flowers. As has previously been explained in *Wrightia* (pp. 50–51), Rafinesque seems to have "stolen" the idea for his species *Triodanis scabra* from Nuttall's annotated specimen, and it is entirely possible that the idea of the genus itself was not original with Rafinesque.

Nuttall's genera *Dysmicodon* and *Campylocera* were taken up by John Torrey, who was anything but eccentric and who apparently espoused Nuttall's proposals with full realization of what he was doing, for he had used the name *Specularia* in his earlier publications and formally designated the American species as a

<sup>1</sup> *Trans. Am. Phil. Soc. n.s. 8: 255. 1843.*

distinct group, sect. *Triodallus*.<sup>1</sup> Torrey seems to have been using *Campylocera* as late as 1870, if one may judge by his annotation on Palmer's no. 168, *Triodanis Holzingeri*, now in the U. S. National Herbarium.

More widespread recognition and use of the names *Dysmicodon* and *Campylocera* was doubtless prevented by the influence of Asa Gray, who published a footnote-monograph on "*Specularia*" in 1876<sup>2</sup>; *Campylocera* was used by C. C. Parry in a paper published in 1872<sup>3</sup>, but so far as I am aware no one publicly questioned the integrity of the inclusive *Specularia* from that time until the days of E. L. Greene.

I should like to close this paper with an illustration from another group of the *Campanulaceae*, the subfamily *Lobelioideae*, in order to emphasize once more the fact that campanulaceous genera (and most other genera, as far as my observations go) in the great majority are founded not solidly upon strong morphological separations, but solidly upon what appear to be natural combinations of characters, in the tradition of Alphonse DeCandolle.

Recent opinions estimate the number of genera of *Lobelioideae* in North and South America together at about 12 to 15 (excluding *Cyphioideae*)<sup>4</sup>. From all the others *Lysipomia* and *Downingia* stand clearly apart as independent genera differentiated by strong morphological characters. *Howellia* is a monotypic, aquatic genus of restricted distribution, distinct because of its seeds which are several times larger than in any other known genus of the family. All the remaining lobeliaceous genera (12 according to one estimate) can be referred to *Lobelia* (those with capsular fruits) or to *Centropogon* (those with baccate fruits) without significant additions to the morphological features of these genera as currently understood! These minor genera may be founded upon a single character (e. g. *Heterotoma*) or upon an assemblage of weak characters (e. g. *Diastatea*); some are doubtless real entities deserving of recognition, others are so weak that hardly more than tradition keeps them alive, but even these border-line

<sup>1</sup> Fl. N. Y. 1: 428. 1843. For use of *Dysmicodon* and *Campylocera* see Rep. Pac. R. R. Surv. 4: 116. 1857, and Rep. Mex. Bound. Surv. 108. 1859.

<sup>2</sup> Proc. Am. Acad. 11: 81-83.

<sup>3</sup> Rep. Hayden Surv. 1870 [4th Ann. Rep. U. S. Geol. Sur. Terr.]: 486.

<sup>4</sup> North Am. Flora 32A<sup>1</sup>: 1-134. 5Ja 1943; Das Pflanzenreich IV. 276b (heft 106): 37-40. 25My 1943.

genera can hardly be merged with their supposed relatives until we know more about what a genus really is, and how it is constituted. *Triodanis*, in my opinion, is as well founded as the average genus in its family, and should be maintained unless we are to have a very severe general reduction in the number of genera recognized in the *Campanulaceae*.

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## A NOVA SCOTIAN DWARF SHADBUSH

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AMELANCHIER **lucida** (Fernald), stat. nov. *A. stolonifera* Wiegand, var. *lucida* Fernald in RHODORA, xxiii. 267 (1921).

When this shrub of sandy or peaty barrens and gravels of Nova Scotia was described I placed it with *A. stolonifera* Wiegand, not then fully understanding how constant (except in hybrids) is the presence of dense tomentum on the summit of the ovary, this character practically invariable in the following stoloniferous or surculose species in eastern North America: *A. alnifolia* Nutt., *A. humilis* Wiegand, *A. mucronata* Nielsen, *A. gaspensis* (Wiegand) Fernald & Weatherby, *A. stolonifera* Wiegand and *A. Fernaldii* Wiegand. When the lustrous-leaved shrub of Nova Scotia was discovered by Long and me I wrote:

one of the neatest little shad bushes we ever saw, a beautiful shrub with stoloniferous habit, low stature (3–6 dm.) and nearly orbicular dark-green, highly lustrous leaves. Afterward, at Grand Lake, Halifax County, at Springhill Junction in Colchester County, at Middleton in Annapolis County and at various places westward we found it a thoroughly distinct and dominant shrub of barrens, either dry or wet. In habit it resembles *A. stolonifera* Wiegand,<sup>1</sup> a characteristic shrub from Maine to Virginia and in eastern Newfoundland, with dull and pale-green or glaucous foliage and with the summit of the ovary densely tomentose; but this characteristic Nova Scotian shrub with dark, glossy leaves has the summit of the ovary wholly glabrous, though it is sometimes arachnoid or sparsely pubescent. Typical *A. stolonifera* we found in Nova Scotia, though only once; but the common shrub is so well marked that it should be separated as a variety.—Fernald, l. c. 130 (1921).

The dark green and lustrous coriaceous leaves are so unlike those of *Amelanchier stolonifera* that the shrub can not properly

<sup>1</sup> Wiegand in RHODORA, xiv. 144 (1912).